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MOLLUSCS AND CLIMATE WARMING IN A LOW MOUNTAIN RANGE NATIONAL PARK

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ABSTRACT

Species restricted to the higher altitudes of low mountain ranges in Central Europe are among the species threatened. To quantify the influence of climate warming, we analysed the altitudinal distribution of mollusc species and modelled the occurrence and distribution of a high montane species under two scenarios of climate warming. Our analysis is based on samples of 3,437 individuals and 46 species collected at 111 localities. Number of individuals and species decreased with altitude. The slope of this decrease changed between 1,100 and 1,200 m a.s.l., which is the ecotone between mixed montane beech-fir-spruce and high-altitude spruce forests. In contrast to the majority of species and the number of species, the occurrence of *Semilimax kotulae* (Westerlund 1883), a Central European endemic, increased with altitude. Again, we found a change in the slope between 1,100 and 1,200 m a.s.l. Using geostatistical models of local temperature as well as spatial GLMs with Poisson and Gaussian errors, we modelled altitudinal distribution of diversity and species under consideration of environmental variables. Especially habitat age was an important predictor for the abundance of many species. For the high montane species *S. kotulae*, our model predicts a decrease in occurrence and abundance with global warming. Although global warming will lead to an overall increase in number of species, species occurring only at higher elevations, such as the *S. kotulae*, will probably become extinct within the study area.

Key words: altitudinal gradient, Bavarian Forest National Park, extinction risk, habitat tradition, *Semilimax kotulae*, BayesX.

INTRODUCTION

Global warming will lead to a latitudinal and altitudinal reorganization of distributional ranges (Parmesan et al., 1999; Parmesan & Yohe, 2003; Root et al., 2003). In extreme, these reorganizations may lead to a regional or even global extinction of species (Bakkenes et al., 2002; Berry et al., 2002; Thomas et al., 2004; IPCC, 2007a, b), and therefore the understanding of the implications of global warming is among the most important tasks for ecologists and conservationists (Sutherland et al., 2006). Despite considerable advances in our understanding of the relations between climate and species distribution at a global scale (Gaston & Blackburn, 2000; Gillooly & Allen, 2007), our knowledge of the local and regional effects of global warming is limited (Grabherr et al., 1994; Kappelle et al., 1999; Travis, 2002; Schrag et al., 2007).

High mountains show long altitudinal gradients that facilitate investigations on the upwards shifts of altitudinal distributions by climate warming (e.g., Kazakis et al., 2007; Pauli et al., 2007). However, the low mountain ranges of Central Europe, with altitudes less than 1,500 m, comprise in total the largest area of all mountains in Europe (CIPRA, 2007). Furthermore, they harbour a number of species with restricted distribution, some relicts from the ice ages (Limondin, 1992; Varga, 1995). Species restricted to the higher zones of these mountains seem to be vulnerable to local and regional extinctions by climate warming for two reasons (Parmesan, 2006): First, the low maximum altitude restricts the possibility to shift ranges upwards to escape the increase of tem-

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perature (Thomas et al., 2004; Thuiller, 2007). Second, the available area decreases with altitude. Any upwards shift leads to a decrease of habitats, to an increase in fragmentation and therefore to a decrease in population size with considerable risk of extinction by demographic stochasticity.

Community composition, species richness as well as location and size of distributional ranges of molluscs depend in particular on climate and soil (Sternberg, 2000; Tattersfield et al., 2001; Aubry et al., 2005; Kappes, 2005; Müller et al., 2005a). This close correlation of mollusc distribution and habitats is in part due to their low dispersal propensity (Waldén, 1981), and therefore molluscs should react very sensitive to global warming. Several species of molluscs are restricted to the upper zone of Central European low mountain ranges (Uminski, 1983). Most of these species are adapted to cold climates, and warming may force a shift of altitudinal distribution with the associated risk of extinction. Beyond this pessimistic scenario, the extinction of local populations may have negative genetic consequences for surviving species. The low dispersal propensity of molluscs leads to considerable genetic variation between populations (Marten et al., 2006). Similar to plants (Matthies et al., 2004), some of this variation may be adaptive (Calosi et al., 2008). The extinction of local populations will probably lead to a reduction in genetic diversity.

Several national parks were established to protect the unique fauna and flora restricted to higher altitudes of the low mountain ranges. The oldest of these national parks in Germany is the Bavarian Forest National Park. Climate warming, however, compromises the protection of high montane assemblages, a major conservation objectives in this and similar parks, of species. Even though the park authorities are unable to influence climate change, it is essential to understand the influence of global warming on the species and habitats for two reasons: Firstly, only if one has some knowledge about species turn-over due to global warming, one is able to detect additional threats. Secondly, the maintenance of habitat diversity is a possibility to decrease the extinction risk due to climate change. Therefore, it is necessary to understand the key resources of the species under consideration to mitigate the effects of climate change. Our study has therefore three main aims:

(1) To assess the influence of altitude and associated environmental variables on number of species and abundance of single species of molluscs in the Bavarian Forest National Park.
(2) To test the influence of site-specific habitat factors on diversity and occurrence of molluscs.
(3) To quantify changes in the extinction risk of high montane species with global warming.

METHODS

Study Area and Study Sites

The Bavarian Forest National Park is located in the southeastern corner of Bavaria, at the border to the Czech Republic (Fig. 1). The park covers approximately 24,000 ha at elevations from 650 m to 1,430 m a.s.l. Total annual precipitation is between 1,200 mm and 1,800 mm depending on altitude. Mean annual temperature (1970–2003) varies between 3.8°C and 5.8°C (Bässler, 2004). Geologically, the Bavarian Forest is the southwestern part of the Bohemian Massif, consisting of granite and gneiss and therefore acidic soils (Table 1). Depending on local conditions, above 1,150 m a.s.l. the vegetation is dominated by almost pure spruce *Picea abies* stands, with only a low proportion of beech, *Fagus sylvatica*, and mountain ash, *Sorbus aucuparia* (high montane forest). Below this, stands are dominated by a mixed montane forest of spruce, beech and fir, *Abies alba* (Walentowski et al., 2004). Due to infestation by bark beetles, mainly *Ips typographus*, large areas of forest have died back, and the resulting structure varies widely from stands with an open canopy, dominated by dead wood, to dense, closed stands (Müller et al., 2008).

We sampled molluscs as part of a more comprehensive program to characterise spatial variation of biodiversity. To get representative samples, we established four transects across the altitudinal range of the park. Along these transects we located a total of 293 plots with a distance of 100 m between adjacent plots. For the sampling of molluscs we randomly selected 111 plots that represented the major forest management types across the altitudinal gradient (Fig. 1). It is important to note that plots were not selected in respect to density or species richness of molluscs. Management types ranged from stands where trees infested by bark beetles are still removed, through stands where management by the forest authorities stopped with the establishment of the national park in 1970, to old-growth forest with veteran trees.

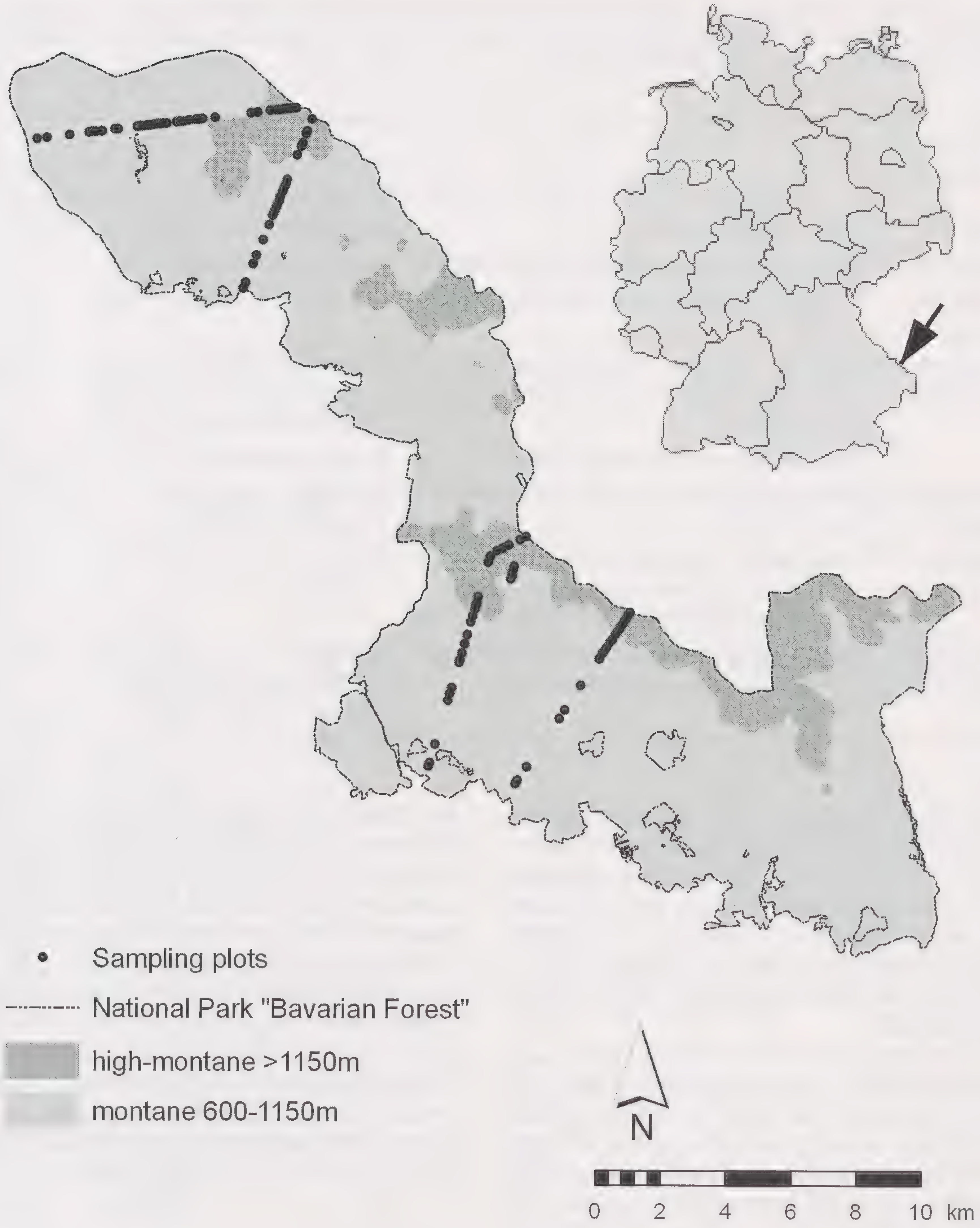

FIG. 1. Study area and location of the 111 plots used to sample molluscs along four altitudinal transects within the Bavarian Forest National Park.

Sampling Methods

Sampling during only one period of the year is not appropriate for all species of molluscs and, for example, early autumn appears to be the best time to sample montane molluscs (Uminski, 1975). Therefore, we used two methods. Firstly, installation of one pitfall traps for three weeks in July 2006 in the centre of each plot. Secondly, hand collection for 30 minutes of all individuals of live snails and slugs within a 0.1 ha area around the centre of each plot in September 2006. Sampling included a few small ephemeral water bodies within forest stands, where we found two *Pisidium* species. When it was not possible to identify an individual in the field, it was stored in 80% ethanol and identified in the laboratory using morphological characters (Wiktor, 1973; Kerney et al., 1983; Jungbluth et al., 1992; Wiktor, 2000). For

TABLE 1. Definition, source and measurement of the environmental variables used for the analysis of abundance, number of species and species richness of terrestrial gastropods and two *Pisidium* spec. within the Bavarian Forest National Park.

Environmental variable	Description	Source	Range total
Altitude	Height above sea level	Surface terrain model	655–1,419 m
Temperature	Mean annual temperature 2000–2007	ArcEcmo modelling	4.1–7.8°C
pH value of humus layer	pH value of humus layer (Bässler et al., 2008)	Laboratory analysis in 2006	2.3–4.42
Soil water balance index	Soil water balance calculated after Ewald et al. (2000) on a scale between 0 (dry) and 10 (wet)	Inspection of characteristics of the top soil as well as pH measurements in 2006	0.0–9.6
Age	Oldest tree in each sample plot	Forest inventory in 2002	49–400 years
Coarse woody debris	Amount of dead wood > 12 cm within 0.1 ha x 10	Inventory of plots along transects in 2006	0–708 m^3 ha^{-1}
Opening of canopy layer	Percentage of signals arriving at 1 m above ground averaged across the 0.1 ha sampling plots (Hyde et al., 2006)	Airborne laser scanning in 2006	0.0–96.8%
Plant species diversity	Shannon index of plant species (without moss) diversity in the field layer	Vegetation mapping in July 2006 using the Londo-scale (Londo, 1976)	0.0–3.13

all subsequent analyses, we totalled numbers of all individuals (abundance) and number of species across the two approaches. Species richness was estimated using the residuals from the regression of number of species versus individuals (Gotelli & Colwell, 2001). Technically, we used the number of individuals as a covariate.

For each plot, GPS coordinates were used to extract altitude from topographic maps and a terrain model of the park. To obtain reliable data for temperature and humidity, 30 data loggers were installed on representative sites across the altitudinal gradient during 2006. Additionally, we used data from five meteorological stations in the region that operated since 2000 to adjust the data collected in 2006 to the average between 2000 and 2007. Values for temperature are higher than those reported in our general description of the area, which refer to the period 1970–2003. With these data, we developed a model, using geostatistical modelling with ArcEGMO (Becker et al., 2002; Pfützner, 2002), to predict for each plot the mean annual temperature, using independent variables extracted from the terrain surface model (a detailed description is available on request by JM). These predicted values were used in all subsequent analyses. A complete list of environmental variables used for modelling the distribution of species is given in Table 1. Although precipitation is an important environmental factor for molluscs, we did not routinely consider precipitation during our study for three reasons. Firstly, we found a high co-linearity of temperature and precipitation (r = 0.71). Second, the scenarios of climate warming predict a decrease in precipitation by only 6% (Spekat et al., 2007). Third, for one species (*Semilimax kotulae*) we included beside temperature precipitation to check our results. However, conclusions were almost identical and therefore we concentrate on temperature.

Statistical Analyses

The plots of number of individuals and number of species *versus* altitude showed considerable scatter. However, a visual inspection suggested a clear pattern of the maximum values. Therefore, to visualize the trends with altitude, we used additive quantile regression smoothing (Koenker et al., 1994) as implemented in the package “quantreg” in R 2.6.0 (Koenker, 2007; $\tau = 0.8$).

To analyse the relationships of total number of individuals, the number of species, species richness and abundance of single species we used generalized linear models (GLM). For

TABLE 2. Results of spatial GLM for species which occurred within at least ten plots of the 111 sampled plots. Black triangles indicate significant influence (*p < 0.05, **p < 0.01, ***p < 0.001), up means positive estimator, down negative estimator. To allow for direct comparisons of the estimators the predictors were standardised to a mean of zero and a variance of 1. Empty triangles indicate marginal significant effects (p < 0.1). Number of species is the number of species per sampling area whereas for the estimation of species richness we included number of individuals as a covariable. Altitudinal distributions of species given in Figure 2.

Dependant variable	Red data book	Frequency (occupied plots)	Temperature	pH-value of humus layer	Soil water balance index	Age	Coarse woody debris	Opening of canopy layer	Plant Diversity
Number of individuals without *S. kotulae*			▲ 10.0**	△ 2.6		▲ 6.9***			
Number of species			▲ 0.29*		▲ 0.10**	▲ 0.09**			▲ 0.09*
Species richness			▲ 0.17*		▲ 0.09**				▲ 0.09*
Species shown in Fig. 2 (left):									
Arion alpinus Pollonera, 1887	X	23	▲ 1.66**		▲ 0.34*	▲ 0.52*			
Arion silvaticus Lohmander, 1937		32	△ 0.99					▲ 0.59*	▲ 0.38*
Columella aspera Waldén, 1966	X	18	▲ 1.96*						
Discus ruderatus ruderatus (W. Hartmann, 1821)	X	27	▲ 1.79**						▼ -0.43*
Euconulus fulvus (O. F. Müller, 1774)		61	▲ 0.87***		▲ 0.20*	▲ 0.35***		△ 0.24	
Limax cinereoniger Wolf, 1803		94	△ 0.34	▲ 0.16*	▽ -0.13	▲ 0.13*			
Malacolimax tenellus (O. F. Müller, 1774)		79	▲ 1.04**	▲ 0.18***	▼ -0.35***	▲ 0.29***			
Punctum pygmaeum (Draparnaud, 1801)		24	△ 0.69	△ 0.33	▲ 0.36*	▲ 0.53**	▼ -0.51*		

(continues)

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Dependant variable	Red data book	Frequency (occupied plots)	Temperature	pH-value of humus layer	Soil water balance index	Age	Coarse woody debris	Opening of canopy layer	Plant Diversity
Semilimax semilimax (J. Férussac, 1802)		28	▲ 1.06*			▲ 0.31*		▽ -0.38	
Semilimax kotulae (Westerlund, 1883)	X	72	▼ -0.70*						
Species shown in Fig. 2 (right):									
Aegopinella pura (Alder, 1830)		14							
Arion brunneus Lehmann, 1862	X	31			▲ 0.33*		△ 0.34		
Arion rufus (Linnaeus, 1758)	X	10							
Arion subfuscus (Draparnaud, 1805)		112		△ 0.08	△ -0.08	▲ 0.15**			
Cochlodina laminata (Montagu, 1803)		20				▲ 0.52*	▽ -0.72	▼ -1.15*	
Discus rotundatus (O. F. Müller, 1774)		30		▲ 0.59**		▲ 0.64***	▼ -0.55*	△ 0.37	
Eucobresia diaphana (Draparnaud, 1805)		13			▲ 0.81**				
Lehmannia marginata (O. F. Müller, 1774)		90				▲ 0.23***		▼ -0.39**	
Monachoides incarnatus (O. F. Müller, 1774)		16							△ 0.67
Nesovitrea hammonis (Ström, 1765)		40		▽ -0.32		▲ 0.51**			▲ 0.43*
Sum of significance (almost significance)			10 (3)	3 (4)	8 (2)	13	2 (2)	3 (3)	5 (1)

the number of species, species richness and abundance of single species, we used Poisson errors with a log link function and for the total number of individuals of all molluscs we used a Gaussian error with an identity link (Quinn & Keough, 2002; Everitt & Hothorn, 2006). To allow a comparison of the estimators within one model, all predictors were standardised to zero mean-unit variance. To account for spatial autocorrelation we used a semiparametric spatial generalised linear model (Dormann et al., 2007). Thereby spatial autocorrelation is alleviated by including a spatial surface in the regression model. Assuming asymptotic normality of the estimated regression coefficients, confidence bands and p-values can be computed based on the standard deviations obtained from the expected Fisher information matrix. For these calculations we used "BayesX" (Fahrmeir et al., 2004; Kneib & Fahrmeir, 2006; Kneib et al., 2008).

To estimate the influence of climate change on the altitudinal distribution of the montane species *S. kotulae*, we used logistic and Poisson regression as implemented in "BayesX" to predict the occurrence as well as abundance of this species considering all available predictors (Table 1). This analysis showed that only temperature had a significant influence on occurrence and abundance (Table 2).To predict occurrence or density of *S. kotulae* from the temperature of a site, GLMs were fitted to the occurrence (logistic model) and abundance (Poisson model) using current mean annual temperature and excluding spatial effects (see above, inset Fig. 4). Subsequently, we used these models to predict the probability of occurrence and abundance of *S. kotulae* for each plot. In a final step, we increased for each plot the mean annual temperature by the values estimated in two scenarios of global warming (IPCC, 2007a) which predict an increase in the mean annual temperature until 2100 by 1.8°K (optimistic assumptions) and by 4.0°K (pessimistic assumptions). The optimistic global estimate of warming corresponds with local models (Spekat et al., 2007). Local models are not available for the pessimistic scenario. From these temperatures, we predicted the occurrence and abundance of *S. kotulae* across the sampled plots. Finally, predictions based on the temperature based model were plotted against altitude of each plot. We visualized the general trend using a spline fit as a local smoother. We also constructed heuristic confidence bands using pointwise 95% prediction intervals calculated from the standard error of the predictions. The upper and lower limits were again estimated with smoothing splines (the R-script of this method is available by JM). Our predictions rest on the assumption that the temperature increase is the same across the altitudinal range. The analysis of temperature data from 1948 to 2002 by Bässler (2008) showed that this assumption is valid for the study region: he found a temperature increase of 0.01°K year^{-1} at all elevations.

RESULTS

In total we sampled 3,437 individuals of 46 species (Appendix). On single plots individuals ranged from 7 to 96 individuals representing 3 to 27 species. In the analysis of community characteristics as well as abundances of the more common species (at least ten occupied plots) *versus* environmental variables, the number of species and individuals, as well as the abundance of 11 species increased with tree age (Table 2). Temperature ranked second, when counting the number of models with a significant temperature effect (Table 2). Seven of the twenty single species models showed a significant response to temperature (Fig. 2 right, Table 2). Most of these responses were positive, only *Semilimax kotulae* showed a negative response (Fig. 2 right, Fig. 3a, b, Table 2).

Although species richness and abundance of molluscs (excluding *S. kotulae*) decreased with altitude and increased with temperature (Fig. 3c–f), these relationships were non-linear. Similarily, for *S. kotulae* the relationship between abundance and temperature with altitude was also non-linear (Fig. 3a, b). The quantile regression showed always change in the slopes at altitudes between 1,100 m and 1,200 m.

For obvious reasons, temperature decreased with altitude across the sampled plots, however with a number of outliers (Fig. 4). These outliers represent sinks for cold air, at the foot of the mountains. Occurrences of *S. kotulae* at lower altitudes were partly located in those sinks; other records at low altitudes were only from moorland site with cold microhabitats.

As expected, the probability of occurrence of *S. kotulae* decreased with increasing temperature (spatial GLM; $p = 0.03$; for all other variables $p > 0.25$; non spatial glm temperature ($p < 0.001$). The cross-correlogram of the residuals of the model including only the variable temperature indicated that the spatial effect can be ignored for this species (Fig. 4 inset). The predictive model indicated that an increase

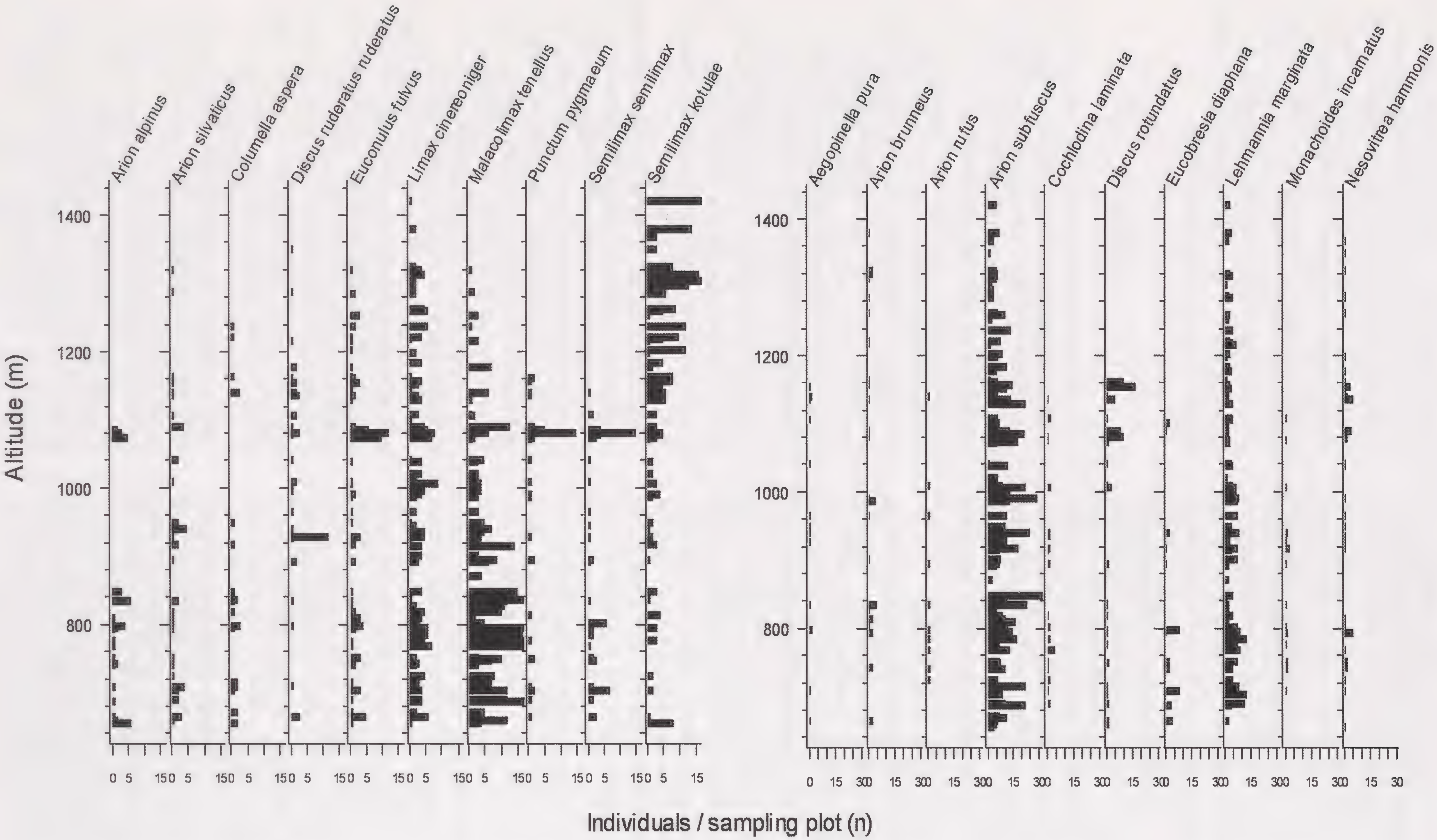

FIG. 2. Abundance of the species, occurring in at least ten sampling plots along altitudinal gradients within the Bavarian Forest National Park (each bar represents one of the 111 plots; see Fig. 1). The upper part shows species where we found at least a marginal significant relationship in spatial glm between abundance and temperature (p < 0.1) Otherwise, species are presented in alphabetical order (see also Table 2).

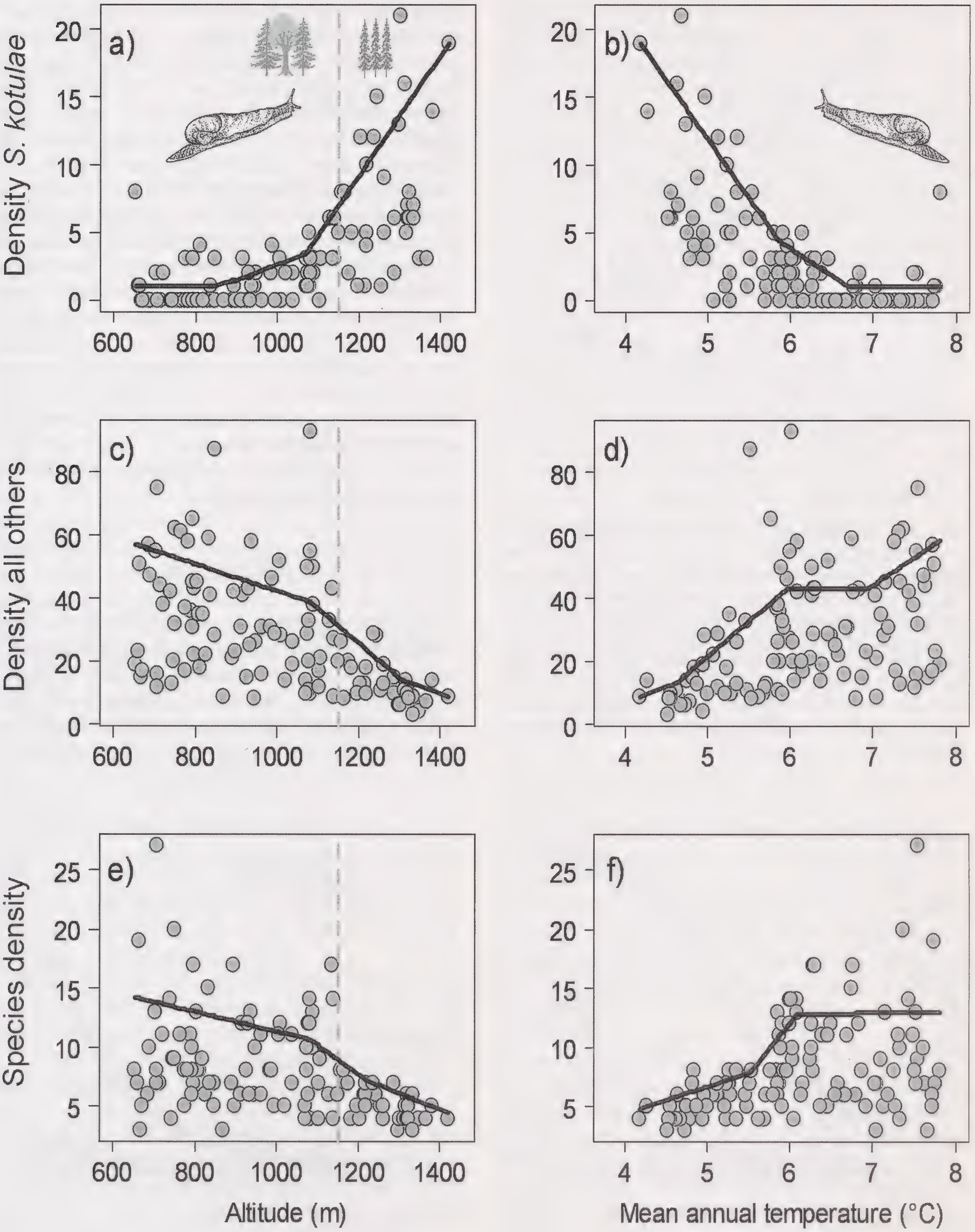

FIG. 3. Number of species, abundance of *Semilimax kotulae* as well as abundance for all species (with exception *S. kotulae*) versus altitude and temperature across 111 plots sampled within the Bavarian Forest National Park (Fig. 1). Lines are additive quantile regressions. The dashed line and the tree symbols indicate the altitude of the change between mixed montane (< 1,150 m) and high montane spruce forests (> 1,150 m).

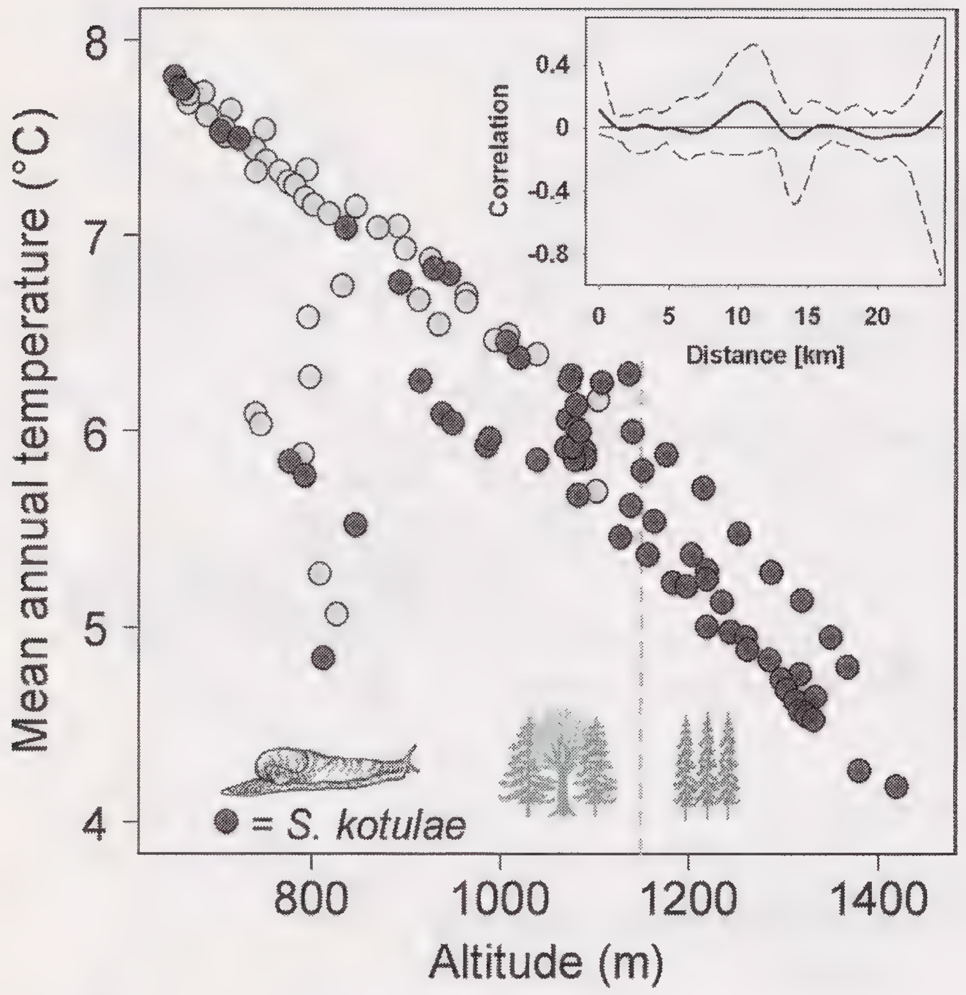

FIG. 4. Relation of mean annual temperature and altitude across the 111 sampling plots in the Bavarian Forest National Park. The outliers are typical sinks for cold air. Dark symbols indicate plots where we recorded *Semilimax kotulae*. Inset shows the spatial autocorrelation of the residuals of a glm with presence/absence data for *S. kotulae* and temperature as predictor. The dashed line indicates the altitude of the change between mixed montane and high montane spruce forests (1,150 m).

in the mean annual temperature of 1.8°K will already lead to a decrease of occurrences by about 50% at altitudes of 1,300 m (Fig. 5). Note that most mountains in the region are below this altitude. Nevertheless, within this optimistic scenario some sinks for cold air at lower altitudes may act as refuges for *S. kotulae* assuming that local circulation patterns of the air will not change with global warming. An increase in mean annual temperature of 4.0°K would probably lead to the extinction of *S. kotulae* in the national park. Modelling abundance produced even more pessimistic results (Fig. 5). Again taking 1,300 m as an example the model predicts abundances of ≈1 if mean annual temperature increases by 1.8°K and close to 0 for an increase of 4.0°K. Note that at present abundances are ≈ 7. These predictions do not change considering temperature and precipitation together.

DISCUSSION

Even though the decrease of diversity along altitudinal gradients has fascinated biologists since Darwin, the reasons are still unclear (Gaston, 2000). We found a non-linear decrease of species richness in molluscs. Aubry et al. (2005) studied richness of molluscs in

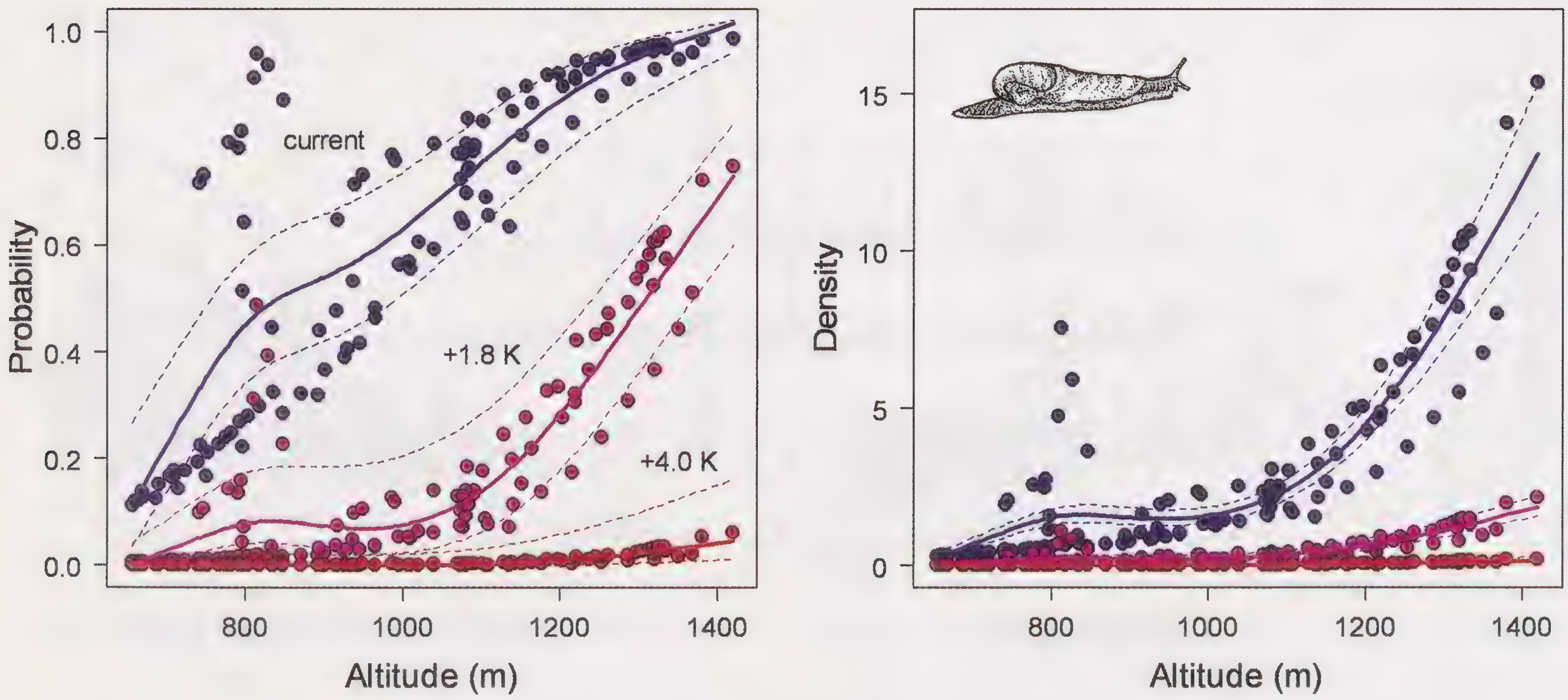

FIG. 5. The blue symbols indicate the predicted probability of occurrences (left) and abundance (right) of *Semilimax kotulae* across the 111 sampling plots versus altitude within the National Park "Bavarian Forest" using annual mean temperature. The blue curves are a local smoother (spline) with heuristic confidence bands (for details see Material and Methods). The other two groups of points and curves are predictions for *S. kotulae* using scenarios of global warming with an increase of the mean annual temperature by 1.8°K and 4.0°K.

calcareous mountains in southeastern France, where they found a plateau of species richness at elevations between 200 m and 1,000 m. Below and above this range they documented a decrease in species richness. Even though this study was undertaken in an area geologically and climatically very much different to our study area, the diversity patterns in our area are rather similar. We found a change in the slope of the decrease of species richness with altitude at around 1,150 m, the altitude where the switch from mixed montane to high montane forests occurs. Several studies have already stressed the close correlation between altitudinal zonation of molluscs and plant communities (e.g., Coppois, 1984).

Körner (2007) noted the difficulty of interpreting effects of non-climatic variables that are strongly correlated with elevation only within certain regions. Such variables can modify altitudinal patterns of diversity in such a way that climate seems to be unimportant (Lee et al., 2004). Nevertheless, Aubry et al. (2005) suggest that climate and the availability of microhabitats determines the number of species. Clearly, our results are consistent with this idea. Temperature, soil water balance, age of trees and plant species diversity are significantly and positively correlated with the densities of several species (Barker & Mayhill, 1999; Müller et al., 2005a; Horsák, 2006). Habitat suitability should be even of more importance in our study area than in the area studied by Aubrey et al. (2005). The sampled region is characterized by acidic soils whereas molluscs often prefer habitats with high pH values (Wäreborn, 1969; Waldén, 1981; Coney et al., 1982; Martin & Sommer, 2004; Horsák, 2006).

Tree age was of overwhelming importance in our models. Furthermore, abundance and number of species also increased with tree age. In forests, the age of the oldest tree in a stand is a surrogate of habitat continuity (Speight, 1989; Sverdrup-Thygeson & Lindenmeyer, 2003; Müller et al., 2005b). Continuity is an important factor for the distribution of molluscs on a regional scale. For example, the abundance of *Limax cinereoniger* and *Macrogastra plicatula plicatula* increases with stand age and therefore habitat continuity (Müller et al., 2005a; Bußler et al., 2007). The importance of continuity for molluscs has at least three components: Firstly, some species feed on the bark of old broadleaved trees and therefore require veterans. Such species are *Clausilia cruciata cruciata* or *Lehmannia marginata*, which at least in Bavaria occurs only in forests (Falkner, 1991; Hässlein, 1966). Secondly, several species need dead wood to obtain calcium, for example *Macrogastra badia crispulata*, *M. plicatula nana*, *Causa holosericea*, *Discus ruderatus ruderatus* (Kappes, 2005; Strätz & Müller, 2006). Thirdly, some mollusc species are consumers of wood-inhabiting or hypogeous fungi (*Arion alpinus*, *Malacolimax tenellus*), which are more common in old stands (Junninen & Angelstam, 2006). Old forests are not only important to molluscs with their low propensity for dispersal (Ant, 1963; Shikov, 1984; Rüetschi, 1999; Strätz, 2005), but also for lichens, wood-inhabiting fungi, saproxylic beetles, or birds (Stubbs, 1989; Bader et al., 1995; Nilsson et al., 1995; Ulikzka et al., 2000; Gustafsson et al., 2004). Our results once more underline the importance of strict forest reserves for conserving the biodiversity of a wide variety of organisms (Christensen et al., 2005).

Overall, we found an increase in number of species and species richness with temperature. This suggests that climate warming will lead to an increase of species richness of molluscs in the national park for two reasons (Grabherr et al., 1994). Firstly, low altitude species will be able to shift the upper distributional limits to higher altitudes. Secondly, new species will be able to invade the area (including such alien species as *Arion lusitanicus*). Therefore, viewed naively, climate warming will be a positive phenomenon if one considers only species richness. However, for species adapted to cool, montane habitats climate warming may lead to local or regional extinction, especially because the available area suitable to them is limited at low mountain ranges. Our example, *Semilimax kotulae*, quantifies this dramatic risk of climate warming.

Semilimax kotulae is endemic to the Alpine-Carpathian area and occurs at altitudes above 600 m. Populations between 500 and 600 m exist in sites where cold air emanates from blocky scree slopes (Hässlein, 1966), which is fully in line with our results. When we compared our data with data from whole Bavaria (Strätz, unpublished) or the East Carpathians (Sulikowska-Drozd & Horsák, 2007), we found a very similar pattern of altitudinal distribution of *S. kotulae*, which suggests that this species may be a suitable indicator for the fate of montane species affected by global warming in whole Central Europe (see also De Groot et al., 1995; Kappelle et al., 1999). As indicated by our exercise presented in Figure 5, an increase in the mean annual temperature of more than 1.8°K will increase the risk of extinction for this species and, if one accepts that *S. kotulae* may be used as an indicator species, of other montane species. Under pessimistic scenarios of climate warming, *S. kotulae* will only survive in regions that provide sufficient habitats at higher altitudes (> 1,300 m; Alps). Note also that the cool plots which at present still harbour populations of *S. kotulae* will also loose their suitability for this species (Fig. 5). The negative response of *S. kotulae* to higher temperatures may have two reasons: for eggs and juveniles a constant humidity is necessary. Humidity decreases with increasing temperature (Uminski, 1975). A second reason may be competition. Even though the biology of *S. kotulae* is still not well known, this species is described as a weak competitor (Falkner, 1991). At lower elevations, four species with similar habitat requirements occur (*Vitrina pellucida*, *Semilimax semilimax*, *Eucobresia diaphana* and *Vitrionobrachium breve*, Falkner, 1991) which may outcompete *S. kotulae.*

During recent years studies have demonstrated that projections produced by alternative models are sometimes such variable that their usefulness for policy decisions is compromised (Araújo et al., 2006). For example, different models predict changes in the distribution from 92% loss to a 323% gain for a South African plant species (Pearson et al., 2006). Such problems call for the application of a combination of modelling techniques (Drake et al., 2006). We checked our results by including additionally precipitation into the model. However, this model produced very similar results. Furthermore, the very similar conclusions from models using presence/absence and abundance data suggest that our conclusion is fairly robust: *S. kotulae* may disappear in the near future from the national park (cf. Berg et al., 2004).

The upper altitudinal zones of the low mountain ranges in Central Europe are not species rich when compared to lowland forests. Nevertheless, several species are restricted to this zone. Most of them are recorded only once or a few times during the last decades (e.g., *Vertigo modesta arctica*, *Vertigo alpestris*), and therefore they are not suited as indicators. Nevertheless their present range of occurrence is between 1,100 m and 1,400 m a.s.l., and these species are faced with a similar risk as *S. kotulae*. Overall global warming constraints one of the major aims of the Bavarian Forest National Park: the conservation of species assemblages of the high montane zone.

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APPENDIX

Species *versus* plot matrix. Numbers indicate individuals; Temp gives the modelled temperature for each plot based on geostatistical modelling see Methods. Note, that two species of genus *Pisidium* which were sampled in a few small ephemeral water bodies within forest stands were also included.

Plot	Temp (in °C)	NN (in m)	*Acanthinula aculeata*	*Aegopinella nitens*	*Aegopinella pura*	*Arianta arbustorum*	*Arion alpinus*	*Arion brunneus*	*Arion distinctus*	*Arion lusitanicus*	*Arion rufus*	*Arion silvaticus*	*Arion subfuscus*	*Balea perversa*	*Boettgerilla pallens*	*Carychium tridentatum*	*Causa holosericea*	*Clausilia cruciata cruciata*	*Cochlicopa lubrica*	*Cochlodina laminata*	*Columella aspera*	*Columella edentula*	*Deroceras laeve*	*Deroceras reticulatum*	*Discus rotundatus*	*Discus ruderatus ruderatus*	*Eucobresia diaphana*	*Euconulus fulvus*	*Isognomostoma isognomostomos*	*Lehmannia marginata*	*Limax cinereoniger*	*Macrogastra plicatula nana*	*Malacolimax tenellus*	*Monachoides incarnatus*	*Nesovitrea hammonis*	*Nesovitrea petronella*	*Oxychilus cellarius*	*Petasina edentula liminifera*	*Pisidium casertanum*	*Pisidium personatum*	*Punctum pygmaeum*	*Radix labiata*	*Semilimax kotulae*	*Semilimax semilimax*	*Vertigo pusilla*	*Vertigo substriata*	*Vitrea subrimata*	*Vitrina pellucida*
T1_27	6.27	798.08			2		4	1			1		9			1					1				1	1	8	4		2	1		2		1				2					2				
T1_3	6.08	741.62					2	2	1	3			7		1	3							2	1				2							2		1		5			10						
T1_30	6.74	833.67			1		6	5			1	2	23								1				1	1		1		2			12	1		1								1				
T1_39	6.58	796.92										1	7								3				1						3		5											2				
T1_4	6.03	746.10					1						4			1														1	1		7	1	1									3				
T1_49	7.05	891.47											5													2		2		2	3		6											1				
T1_51	6.87	926.06			1								4													1		1		2	1		4											1				
T1_52	6.80	945.35											1																	1	2		3										1	1				
T1_53	6.69	964.28			1			1			1		11			2												1		7	2		3		1									1				
T1_55	6.48	1009.63									1	1	9			1									1	2		1		5	2		3								1			1				
T1_56	6.39	1040.28			1							2	1												1	1				4	1		5		1						1			1				
T1_58	6.15	1104.93			1							1	5													2				5	1		2															
T1_59	5.99	1140.64			2						1	1	6			1									1	2		1		2			6		2						1		3	1				
T1_60	5.87	1176.55											5													2		1		4			7		1								2					
T1_61	5.70	1215.29											2													1		1		6			3										1					
T1_62	5.47	1253.49											3															3		2			3										1					
T1_63	5.27	1287.09										1	3													1				2			2		1								2					

(continues)

(continued)

Plot	Temp (in °C)	NN (in m)	*Acanthinula aculeata*	*Aegopinella nitens*	*Aegopinella pura*	*Arianta arbustorum*	*Arion alpinus*	*Arion brunneus*	*Arion distinctus*	*Arion lusitanicus*	*Arion rufus*	*Arion silvaticus*	*Arion subfuscus*	*Balea perversa*	*Boettgerilla pallens*	*Carychium tridentatum*	*Causa holosericea*	*Clausilia cruciata cruciata*	*Cochlicopa lubrica*	*Cochlodina laminata*	*Columella aspera*	*Columella edentula*	*Deroceras laeve*	*Deroceras reticulatum*	*Discus rotundatus*	*Discus ruderatus ruderatus*	*Eucobresia diaphana*	*Euconulus fulvus*	*Isognomostoma isognomostomos*	*Lehmannia marginata*	*Limax cinereoniger*	*Macrogastra plicatula nana*	*Malacolimax tenellus*	*Monachoides incarnatus*	*Nesovitrea hammonis*	*Nesovitrea petronella*	*Oxychilus cellarius*	*Petasina edentula liminifera*	*Pisidium casertanum*	*Pisidium personatum*	*Punctum pygmaeum*	*Radix labiata*	*Semilimax kotulae*	*Semilimax semilimax*	*Vertigo pusilla*	*Vertigo substriata*	*Vitrea subrimata*	*Vitrina pellucida*
T1_64	5.13	1319.59										1	6															1		3			1										7					
T1_65	4.94	1350.04											2													1									1								3					
T1_66	4.78	1367.99											4																	2					1								3					
T1_9	5.87	791.70					1	1				1	11												1			2			1		9	2	5									2				
T2_2	5.84	777.69					1						5												1					7			21	1							1		3					
T2_23	5.06	827.25						1					5															1		2	2		11															
T2_25	4.84	813.40						2					10															1			1		2		1						1		4					
T2_27	5.27	809.53					1					1	16															3		2	4		2						6									
T2_3	5.77	794.09					2			1			15															1		9	5		32										3					
T2_35	6.26	916.17	1									2	18							2	1						1	2		7			3	3	1								3					
T2_36	6.09	938.89			1	2						5	25					1		2						1	2			8	2		7	2									1					
T2_38	6.03	949.31			1							2	10								1							1		4	1		5		1								2					
T2_41	5.92	986.54						4					13															1		7	2		3								1		2					
T2_44	5.96	990.01						1					29															2		8	4				1						1		4					
T2_48	5.85	1039.44											12															1		5	4		3		1								2					
T2_50	5.67	1082.01											6																		1		3										2					
T2_52	5.45	1128.13											22															1		5	4		1										6					
T2_53	5.36	1157.20						1					15															1		3	4				1						1		8					
T2_54	5.22	1183.69											11																	3	4												5					
T2_67	4.18	1419.52											5																	3	1												19					
T2_69	4.26	1380.01						1					7																	4	2												14					

(continues)

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Plot	Temp (in °C)	NN (in m)	*Acanthinula aculeata*	*Aegopinella nitens*	*Aegopinella pura*	*Arianta arbustorum*	*Arion alpinus*	*Arion brunneus*	*Arion distinctus*	*Arion lusitanicus*	*Arion rufus*	*Arion silvaticus*	*Arion subfuscus*	*Balea perversa*	*Boettgerilla pallens*	*Carychium tridentatum*	*Causa holosericea*	*Clausilia cruciata cruciata*	*Cochlicopa lubrica*	*Cochlodina laminata*	*Columella aspera*	*Columella edentula*	*Deroceras laeve*	*Deroceras reticulatum*	*Discus rotundatus*	*Discus ruderatus ruderatus*	*Eucobresia diaphana*	*Euconulus fulvus*	*Isognomostoma isognomostomos*	*Lehmannia marginata*	*Limax cinereoniger*	*Macrogastra plicatula nana*	*Malacolimax tenellus*	*Monachoides incarnatus*	*Nesovitrea hammonis*	*Nesovitrea petronella*	*Oxychilus cellarius*	*Petasina edentula liminifera*	*Pisidium casertanum*	*Pisidium personatum*	*Punctum pygmaeum*	*Radix labiata*	*Semilimax kotulae*	*Semilimax semilimax*	*Vertigo pusilla*	*Vertigo substriata*	*Vitrea subrimata*	*Vitrina pellucida*
T2_73	4.76	1317.97						1					6																	5	2												5					
T2_75	4.83	1285.57						1					4															2		5	2				1								6					
T2_79	5.29	1218.65						1					2															1		5	1												5					
T2_81	5.36	1202.83											9															1		3													12					
T2_9	5.52	847.50					3						60															1		4	4		15										3					
T3_1	7.81	655.00					6						4								2							1			1		4		1								8					
T3_12	7.64	714.98											22								2				1			1		8	3		7															
T3_17	7.54	750.19										1	8									3			2		2			3	1		10								2							
T3_22	7.33	795.42											12								1				1		1	2		5	6		15	1	1													
T3_23	7.32	812.49											7																				1										1					
T3_25	7.14	846.87											8								1									5	4		10															
T3_26	7.04	870.08											3																	2			4															
T3_27	6.93	900.20						1					8																	7	4		3															
T3_28	6.83	929.44										1	11													12		3		3	5		4	1	1						1		2	1				
T3_29	6.65	964.35											2													1		1		7	2		3															
T3_3	7.75	660.02					2					1	5												2						1		12										1					
T3_30	6.46	994.48											13													1				6	5		4															
T3_31	6.37	1020.19											6																	1	4		3										2					
T3_33	6.06	1072.47											7																		5		2										3					
T3_34	5.89	1089.60										4	13												8	1		2		2	5		13								2		3					
T3_35	5.86	1090.18						1				2	10												3	1	1	2		1	2		10		4						1		2					

(continues)

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Plot	Temp (in °C)	NN (in m)	*Acanthinula aculeata*	*Aegopinella nitens*	*Aegopinella pura*	*Arianta arbustorum*	*Arion alpinus*	*Arion brunneus*	*Arion distinctus*	*Arion lusitanicus*	*Arion rufus*	*Arion silvaticus*	*Arion subfuscus*	*Balea perversa*	*Boettgerilla pallens*	*Carychium tridentatum*	*Causa holosericea*	*Clausilia cruciata cruciata*	*Cochlicopa lubrica*	*Cochlodina laminata*	*Columella aspera*	*Columella edentula*	*Deroceras laeve*	*Deroceras reticulatum*	*Discus rotundatus*	*Discus ruderatus ruderatus*	*Eucobresia diaphana*	*Euconulus fulvus*	*Isognomostoma isognomostomos*	*Lehmannia marginata*	*Limax cinereoniger*	*Macrogastra plicatula nana*	*Malacolimax tenellus*	*Monachoides incarnatus*	*Nesovitrea hammonis*	*Nesovitrea petronella*	*Oxychilus cellarius*	*Petasina edentula liminifera*	*Pisidium casertanum*	*Pisidium personatum*	*Punctum pygmaeum*	*Radix labiata*	*Semilimax kotulae*	*Semilimax semilimax*	*Vertigo pusilla*	*Vertigo substriata*	*Vitrea subrimata*	*Vitrina pellucida*
T3_36	5.85	1079.73						1					7																	1	1		1										1					
T3_37	5.91	1069.87											5																	3			1								1		1					
T3_45	5.69	1102.02											7														2			2	1																	
T3_48	5.62	1139.15											5								3										1												6					
T3_49	5.54	1163.20						1				1	2								1							1		1	1												8					
T3_52	5.24	1219.57						1					8								1							1		3	4												10					
T3_53	5.13	1236.23											14								1							2		5	6		1										12					
T3_57	4.94	1260.55											10																	3	6												5					
T3_9	7.73	686.59					1						22														3			4	4		23															
T4_14	7.67	668.72								1			11																				3															
T4_20	7.53	708.49			1								5					2			2									1	2		3															
T4_21	7.50	709.21		1	1								2					2		1						1				1			3															
T4_22	7.53	703.01										2	9					1			1				1			3	1	12	4		12								2		2	7				
T4_24	7.61	689.91										2	10							2					2			1		11	4		12								1			2				
T4_28	7.75	663.87			1	1	1	2				3	6									2			2	3	4	5		2	6		3					1	5		1		1	3				
T4_29	7.72	669.94											7								2							1			2		5															
T4_35	7.54	707.10					1			13		4	6		1	3		1		1		8		1			8	1		2	1	1	2	1	1	5		2	3		1			2	2	2	1	1
T4_36	7.50	722.71								2	1	1	6					7		2										5	5		8		1								2					
T4_37	7.44	739.53					1			3	1	1	10					5		1		4					2	2		5	2		3	2														
T4_38	7.37	751.68				1	1			7		1	7					3		1		4					2	3		7	2		3	2	2	1		1	10	2				2				
T4_39	7.32	766.85					1			2	1		13							4								1		9	7		21		1									1				

(continues)

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Plot	Temp (in °C)	NN (in m)	Acanthinula aculeata	Aegopinella nitens	Aegopinella pura	Arianta arbustorum	Arion alpinus	Arion brunneus	Arion distinctus	Arion lusitanicus	Arion rufus	Arion silvaticus	Arion subfuscus	Balea perversa	Boettgerilla pallens	Carychium tridentatum	Causa holosericea	Clausilia cruciata cruciata	Cochlicopa lubrica	Cochlodina laminata	Columella aspera	Columella edentula	Deroceras laeve	Deroceras reticulatum	Discus rotundatus	Discus ruderatus ruderatus	Eucobresia diaphana	Euconulus fulvus	Isognomostoma isognomostomos	Lehmannia marginata	Limax cinereoniger	Macrogastra plicatula nana	Malacolimax tenellus	Monachoides incarnatus	Nesovitrea hammonis	Nesovitrea petronella	Oxychilus cellarius	Petasina edentula liminifera	Pisidium casertanum	Pisidium personatum	Punctum pygmaeum	Radix labiata	Semilimax kotulae	Semilimax semilimax	Vertigo pusilla	Vertigo substriata	Vitrea subrimata	Vitrina pellucida
T4_4	7.27	774.83											7															1		3	5		1															
T4_40	7.25	782.44								1	1		17							2										12	6		17											2				
T4_41	7.19	793.14						2					12																	7	4		5											1				
T4_42	7.15	803.04						1				1	12							2		1						1		7	3		5	1	1				4					6				
T4_43	7.10	817.95										1	9							1	1				1			2		5	5		10															
T4_44	7.03	836.09											11								2				1					1	1		25										1					
T4_47	6.75	893.93									1	1	7				4			2		4			2		1			2	1		9	1							2		1	2		2	1	
T4_48	6.67	914.29											7				1			1										4	4		14															
T4_49	6.54	936.08											10							2										2	5		5		1													
T4_51	6.45	1006.87				2							22							3					3	1		1		6	9		4	1									3					
T4_53	6.28	1076.29											15							1					2					3	5		2	1									2					
T4_54	6.24	1108.10											6							3					1					4	3		1	1									3	2				
T4_55	6.29	1135.87			1			1				1	14						1	1					5	3		2		1	3				5						1		3			1	2	1
T4_56	6.17	1153.76			1							1	2												17	2		3			2				3								1				1	
T4_57	6.04	1161.32										1	6	1					1						10	1		2							1						2		3				1	1
T4_59	5.80	1150.50											11															1		4	3				1								5					
T4_7	7.32	742.03											5															1		4	3																	
T4_70	5.21	1197.20											6																	1	2				1								1					
T4_72	4.99	1219.93						1					7																	1	1												4					
T4_76	4.88	1261.64						1					6																		5				1								9					
T4_78	4.72	1297.51											4																		2												13					

(continues)

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Plot	Temp (in °C)	NN (in m)	Acanthinula aculeata	Aegopinella nitens	Aegopinella pura	Arianta arbustorum	Arion alpinus	Arion brunneus	Arion distinctus	Arion lusitanicus	Arion rufus	Arion silvaticus	Arion subfuscus	Balea perversa	Boettgerilla pallens	Carychium tridentatum	Causa holosericea	Clausilia cruciata cruciata	Cochlicopa lubrica	Cochlodina laminata	Columella aspera	Columella edentula	Deroceras laeve	Deroceras reticulatum	Discus rotundatus	Discus ruderatus ruderatus	Eucobresia diaphana	Euconulus fulvus	Isognomostoma isognomostomos	Lehmannia marginata	Limax cinereoniger	Macrogastra plicatula nana	Malacolimax tenellus	Monachoides incarnatus	Nesovitrea hammonis	Nesovitrea petronella	Oxychilus cellarius	Petasina edentula liminifera	Pisidium casertanum	Pisidium personatum	Punctum pygmaeum	Radix labiata	Semilimax kotulae	Semilimax semilimax	Vertigo pusilla	Vertigo substriata	Vitrea subrimata	Vitrina pellucida
T4_79	4.67	1303.55											3																	1	2												21					
T4_80	4.62	1312.11						1					5																		5												16					
T4_81	4.56	1318.54						2					4																		4												6					
T4_82	4.56	1322.92						2					4																		1				1								8					
T4_83	4.54	1325.09						1					5																		2												6					
TS_1	6.13	1080.25					1						10															3			5		1										5					
TS_2	5.91	1076.80					3						9					1							1	1		5			4		2		2						1		5	4				
TS_3	6.01	1081.29					3						16							1					10	3		12		2	8	1	6		1						15		3	15				
TS_4	5.99	1083.80					2						21												3	1		6		2	6		4		1						5		2	4				
TS_5	6.25	1073.47					5						18												2			10		1	7		2								2		1	3				